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SHORTER ARTICLES AND DISCUSSION

PRODUCTION OF PURE HOMOZYGOTIC ORGANISMS FROM HETEROZYGOTES BY SELF-FERTILIZATION

HAS any one worked out formulæ for determining the rate at which organisms become homozygotic through continued self-fertilization? The problem is of interest in various connections, but principally perhaps with relation to the "pure line" work. Johannsen worked, for example, with self-fertilizing beans that are held to be homozygotic in all respects. I have often heard the questions raised: How probable is it that such plants really are homozygotic? Is it indeed possible that they have reached a purely homozygotic condition?

I have not come across a working out of this matter, and finding it necessary to deal with the problem in connection with studies of inheritance in *Paramecium*, it will perhaps be useful if I put on record the results.[1]

The principles which underlie the matter are the following: (1) In self-fertilized organisms, all characteristics that become once homozygotic, remain homozygotic forever after, since there is no method in self-fertilization of introducing a gamete that is diverse in this respect; (2) characteristics heterozygotically represented become homozygotic in a certain proportion of the offspring. The problem becomes essentially this: in what proportion do the heterozygotic characters become homozygotic, and how great a proportion of all the organisms will therefore have become thus homozygotic after a given number of self-fertilizations?

Suppose that we begin with an organism in which all separable characters are heterozygotically represented.

1. Consider first a single pair of such alternative characters, which we may call $\left\{\begin{matrix} A \\ a \end{matrix}\right.$. The gametes produced will be A, a,

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[1] At the moment of receiving the proof of this note I receive also the masterly paper of East and Hayes ("Heterozygosis in Evolution and in Plant Breeding," Bulletin 243, Bureau of Plant Industry, June 5, 1912), in which this matter is dealt with and a general formula given. "The probable number of homozygotes and any particular class of heterozygotes in any generation r is found by expanding the binomial $[1 + (2^r - 1)]^n$, where n represents the number of character pairs involved," etc. (p. 21). Possibly the present note may still be useful.

A, and a, and when these combine in all possible ways, they give zygotes $AA + Aa + aA + aa$; that is, two homozygotes and two heterozygotes. Thus, the self-fertilization of such an organism gives $\frac{1}{2}$ the progeny homozygotic (with respect to this characteristic); $\frac{1}{2}$ heterozygotic. If we let $x =$ the proportion of homozygotes, y the proportion of heterozygotes (with respect to one character), then after the first self-fertilization

$$x = \tfrac{1}{2} \text{ of all.}$$
$$y = \tfrac{1}{2} \text{ of all.}$$

Now, after the next self-fertilization, of course the homozygotes x remain pure, so that half of all the progeny are still homozygotes on this account. The heterozygotes y of course again break up, in the way already set forth, one half into x, the other half remaining y. Since y included half of all, this will give $\frac{1}{2}$ of $\frac{1}{2}$ ($= \frac{1}{4}$ of all) as x, $\frac{1}{2}$ of $\frac{1}{2}$ ($= \frac{1}{4}$ of all) as y.

So the total proportion for the homozygotes x becomes after the second fertilization

$$x = \tfrac{1}{2} + (\tfrac{1}{2})^2 = \tfrac{3}{4},$$

while

$$y = (\tfrac{1}{2})^2 = \tfrac{1}{4}.$$

This process is repeated after each fertilization, so that if there are n fertilizations in succession, the total number of homozygotes x, becomes

$$x = \tfrac{1}{2} + (\tfrac{1}{2})^2 + (\tfrac{1}{2})^3 \ldots \text{ up to } (\tfrac{1}{2})^n.$$

This expression reduces to $x = \dfrac{2^n - 1}{2^n}$, where n is the number of fertilizations.

For the heterozygotes, y, on the other hand the formula is simply

$$y = (\tfrac{1}{2})^n.$$

These then are the formulæ in case we deal with but one pair of characters. They express (1) the proportion of all the organisms that will be homozygotic (or heterozygotic as the case may be), after a given number n of fertilizations; (2) also they of course express the relative probability for a given case, as to whether it shall be homozygotic or heterozygotic.

2. When we are to deal with two or more pairs of characters, the problem may be attacked in two ways. One is by the general principles of probabilities; the other is by analyzing the case of two or more characters in the way exemplified above. The two methods give the same results.

The first method is far the simpler. It is merely an application of the principle that when we know the probability for each of two or more things separately, the probability that all of them shall happen is the product of the separate probabilities for each. Now, we know that the probability x for the homozygotic condition with respect to one character is

$$x = \frac{2^n - 1}{2^n}.$$

For two characters it is then

$$\left(\frac{2^n - 1}{2^n}\right) \times \left(\frac{2^n - 1}{2^n}\right); \quad \text{or} \quad \left(\frac{2^n - 1}{2^n}\right)^2.$$

For three characters it is of course $\left(\frac{2^n - 1}{2^n}\right)^3$, and in general, for any number m of characters, the probability x for pure homozygotes (or the proportional number of pure homozygotes) is

$$x = \left(\frac{(2^n - 1)^m}{2^n}.\right)$$

By similar reasoning, the proportion of all the organisms that will be heterozygotic with respect to all the m characters is

$$y = (\tfrac{1}{2})^{nm}.$$

With two or more characters, there will be of course a considerable number of the organisms that are homozygotic with respect to some characters, heterozygotic with respect to others. If we call the proportion of these z, then

$$z = 1 - (x + y).$$

And if we let v be the total proportion that contains any heterozygotic characters (so that $v = y + z$), then

$$v = 1 - \left(\frac{2^n - 1}{2^n}\right)^m = \frac{2^{mn} - (2^n - 1)^m}{2^{mn}}.$$

These formulæ may readily be deduced algebraically, or verified, by a detailed analysis of a case of two or more characters. It may be worth while to indicate the method followed, by taking up the simpler case of two pairs of characters. Call these $\left\{\begin{matrix} A \\ a \end{matrix}\right.$ and $\left\{\begin{matrix} B \\ b \end{matrix}\right.$. The gametes formed are AB, Ab, aB, and ab. When these combine in all possible ways (as indicated in the diagrams given in Bateson's Mendelism), these give the following results:

$$1ABAB + 1AbAb + 1aBaB + 1abab + 2ABab + 2AbaB + 2ABAb + 2ABaB + 2Abab + 2aBab = 16.$$

It will be observed that of the entire 16, the first four are pure homozygotes, the second four are pure heterozygotes (heterozygotic with respect to both characters); while the last 8 are mixed (homozygotic with respect to one character, heterozygotic with respect to the other). Letting $x =$ pure homozygotes, $y =$ pure heterozygotes, $z =$ mixed, we find thus that

$$x = 1/4,\ y = 1/4,\ z = 1/2, \text{ of all.}$$

Now, by an analysis of the sort already given, it will be found that at the next self-fertilization, x remains x; y breaks up, 1/4 of these becoming x, 1/2 becoming z, and 1/4 remaining y; z breaks up, 1/2 of these becoming x, 1/2 remaining z.

Now, when we recall that before the second fertilization x was 1/4; y, 1/4, and z, 1/2 of all, we see from the above that after the second fertilization

$$x = 1/4 + (1/2 \times 1/2) + (1/4 \times 1/4) = 9/16 = \left(\frac{2^n - 1}{2^n}\right)^2,$$
$$y = (1/4 \times 1/4) = 1/16 = (1/2)^{2n},$$
$$z = (1/2 \times 1/2) + (1/2 \times 1/4) = 3/8 = (1/2)^n + (1/2)^{n+1}.$$

These are the same formulæ for x and y that were obtained by the other method (since here n and m are each 2). This method however gives in addition a direct formula for z.

It is easy to verify the formulæ for three pairs of characters, though of course the conditions become here somewhat more complex.

We may now summarize our formulæ, and show the results they give in certain examples.

Let $x =$ the proportional number of organisms that are pure homozygotes (with respect to all the characters considered),

$y =$ the proportion that are heterozygotic with respect to all the characters considered,

$z =$ the proportion that are mixed,

$v =$ the proportion that have any heterozygotic characters.

Then, if $n =$ the number of successive self fertilizations and $m =$ the number of pairs of characters,

$$x = \left(\frac{2^n - 1}{2^n}\right)^m, \tag{1}$$

$$y = (1/2)^{mn}, \tag{2}$$

$$z = 1 - (x + y), \tag{3}$$

$$v = 1 - x = \frac{2^{mn} - (2^n - 1)^m}{2^{mn}}. \tag{4}$$

Examples.—(1) Suppose that there have been eight self-fertilizations, and that we are dealing with 10 pairs of characters. What proportion x of the organisms will be homozygotic with respect to all the 10 characters? What proportion will be homozygotic with respect to any given one character? To any two or three?

Taking first the case for the entire 10 characters, by formula (1)

$$x = \left(\frac{2^8-1}{2^8}\right)^{10} = \left(\frac{255}{256}\right)^{10} = \log.\ 9.9830020 = .961617.$$

Thus, out of 100 individuals, somewhat above 96 would be pure homozygotes; or by formula (4), but one in 26 would be heterozygotic in any respect ($v = .038383$).

With respect to any one character formula (1) gives

$$x = \left(\frac{2^8-1}{2^8}\right)^{1} = \frac{255}{256} = .99609375,$$

so that all but 4 in 1,000 would be homozygotes with respect to that character.

In the same way we find that with respect to any two characters the proportion of homozygotes would be .9922; with respect to three, .9883; with respect to four, .9845, etc.

(2) Suppose that there are 20 pairs of characters, and that there have been 20 self-fertilizations. Then

$$x = \left(\frac{2^{20}-1}{2^{20}}\right)^{20} = \left(\frac{1{,}048{,}575}{1{,}048{,}576}\right)^{20} = \log.\ 9.9999957 = .999998.$$

That is, of a million individuals, all but two would be pure homozygotes.

It thus appears that if the number of separably heritable characters is not very great (say not above 100), while the organism has been self-fertilized for many generations, it is to be expected that practically all of the organisms will be homozygotic with respect to all their characters, they will be "pure homozygotes."

H. S. Jennings

YELLOW AND AGOUTI FACTORS IN MICE NOT "ASSOCIATED"

In a recent number of the American Naturalist Mr. Sturtevant[1] suggests that these two color factors may bear to each other the relation which Bateson has called "repulsion" or "spurious allelomorphism" and which Morgan now includes with "coupling" in a more general category, "association." The supposed

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[1] Sturtevant, A. H., "Is there Association Between the Yellow and Agouti Factors in Mice?" Am. Nat. Vol. XLVI, No. 546, p. 368, 1912.